A NEW HOLOPTYCHIID POROLEPIFORM FISH FROM THE UPPER FRASNIAN OF ELGIN, SCOTLAND

by PER ERIK AHLBERG

ABSTRACT. A new porolepiform, *Duffichthys mirabilis* gen. et sp. nov., is described from the Upper Frasnian locality of Scat Craig, near Elgin, Scotland. *Duffichthys* is a member of the Holoptychiidae, and shares derived characters with *Glyptolepis*, but has a unique lower-jaw morphology characterized by an extremely large parasymphysial tooth plate attachment; two isolated parasymphysial tooth plates, probably belonging to *Duffichthys*, differ from those of other known holoptychiids in carrying only a single fang. The parasymphysial dentition may have played a greater role in prey capture in *Duffichthys* than in other known porolepiforms.

THE Upper Frasnian (House, Richardson, Chaloner, Allen, Holland and Westoll 1977) fossil locality of Scat Craig, near Elgin (Text-fig. 1A), has yielded a fragmentary but rich vertebrate assemblage including many porolepiform specimens. The material, which is preserved in the round and essentially undistorted, was mostly collected during the late 1830s and early 1840s (Andrews 1982): one of the most assiduous collectors was Patrick Duff (1791–1861), Town Clerk of Elgin. In 1841, some porolepiform teeth collected by Duff at Scat Craig were presented to Richard Owen, who used them as the basis for a new genus, *Dendrodus* (Owen 1841). Duff (1842) figured further teeth from the site, together with scales of *Holoptychius* and two fragmentary porolepiform lower jaws. He noted that the latter had been attributed to *Holoptychius nobilissimus* (by an unspecified authority, possibly Hugh Miller), but expressed serious doubts about this identification.

The next worker to examine the Scat Craig porolepiforms in detail was Brown (1978). She studied the scale material, which she attributed to *Holoptychius* and *Glyptolepis*, and figured a very large lower jaw of *Holoptychius* (BMNH P8266), but did not discuss Duff's lower jaws or any of the other porolepiform jaw fragments from Scat Craig.

A recent (Ahlberg 1989) examination of Duff's (1842) jaw fragments, together with two further specimens of the same taxon, has confirmed Duff's suspicion that they do not belong to *Holoptychius*: rather, they represent a previously unknown porolepiform with a very unusual jaw morphology. This new taxon is described below.

SYSTEMATIC PALAEONTOLOGY

Class OSTEICHTHYES Huxley, 1880
Subclass SARCOPTERYGII Romer, 1955
Division POROLEPIFORMES Jarvik, 1942

Diagnosis. A clade defined by the possession of dendrodont teeth (Schultze 1969; Panchen and Smithson 1987) and a unique skull roof pattern in which the intertemporal and supratemporal are absent, the nasal series contributes to the skull roof margin posterior to the orbit, and the postotic sensory canal passes through the growth centre of the postparietal bone.

Systematic note. The clade Porolepiformes includes the primitive genera *Porolepis* and *Heimenia*, and the derived family Holoptychiidae (see below), but not the Lower Devonian forms *Youngolepis* (Chang 1982) and *Powichthys* Jessen, 1975. *Powichthys* was described as a porolepiform (Jessen 1975, 1980; Jarvik 1980), and

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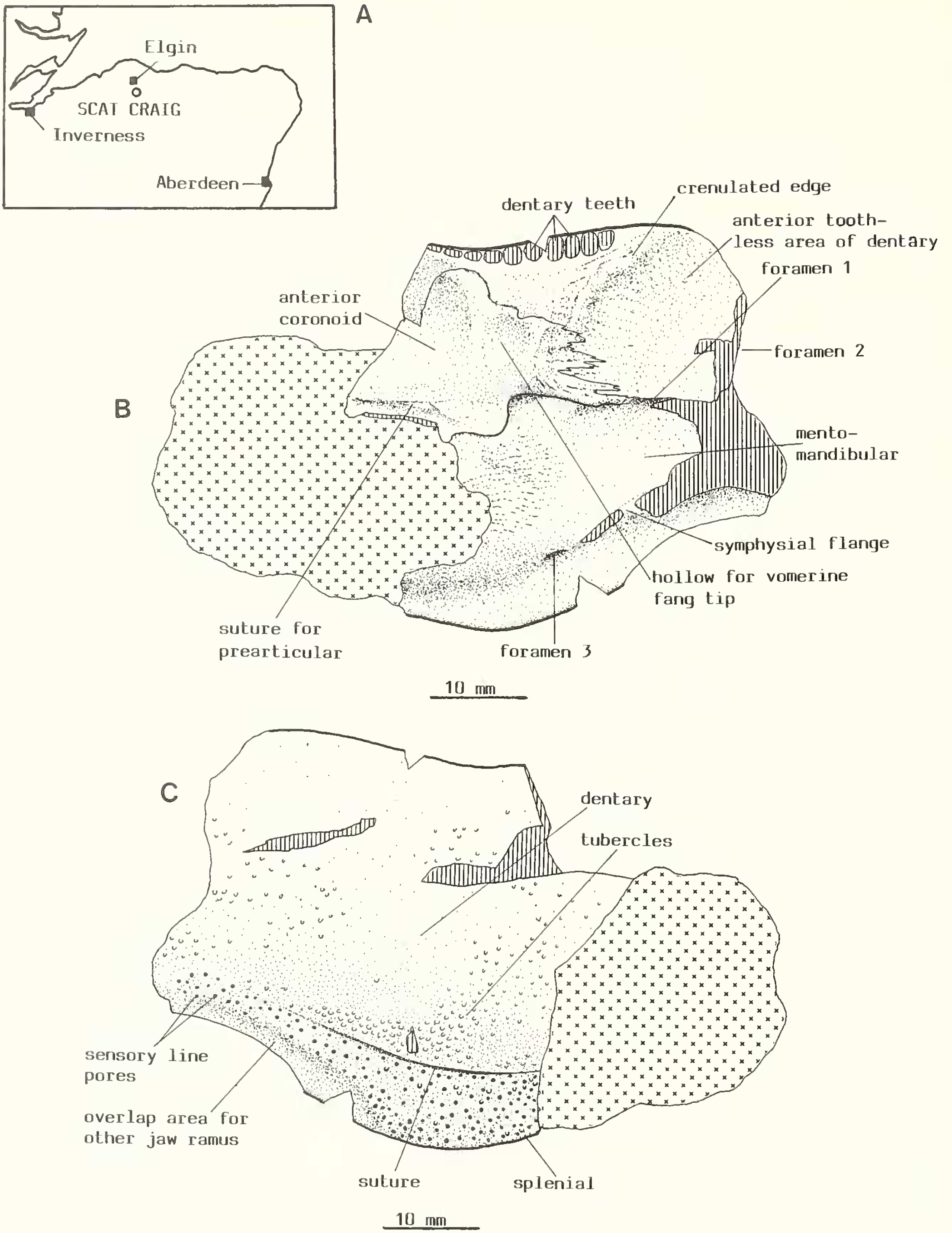

TEXT-FIG. 1. A, map showing the location of Scat Craig in Scotland. B–C, RMS G 1950.38.76, left lower-jaw fragment of *Duffichthys mirabilis* gen. et sp. nov., in mesial and lateral views. Thick outline, true edge; thin outline, broken edge; vertical hatching, broken surface; crosses, matrix.

Chang (1991) regarded both genera as closely related to the Porolepiformes. However, they also share derived characters with lungfishes (Ahlberg 1991; Chang 1991), and their precise relationship to these two groups remains in doubt.

Andrews and Westoll (1970) used the name Holoptychiida in preference to Porolepiformes. Jarvik's (1942) original group name is, however, preferable both on grounds of priority and because it avoids confusion with the family Holoptychiidae (see below).

The Porolepiformes are not very diverse, and in the past the group has usually been given ordinal status (Jarvik 1942; Andrews and Westoll 1970; Schultze and Arsenault 1987). However, as one of the principal subgroups of the Sarcopterygii, its 'rank' is equivalent to that of the Dipnoi or Tetrapoda. The assignation of divisional status to these groups follows Ahlberg (1991).

Family HOLOPTYCHIIDAE Owen, 1860

Diagnosis. A clade within the Porolepiformes defined by the presence of porolepiform character states combined with the absence of cosmine, possession of round scales, loss of the median gular plate and a relatively short ethmosphenoid cranial division.

Systematic note. The Porolepiformes have generally been divided into two families, Holoptychiidae and Porolepidae, by previous authors (Jarvik 1942, 1972; Andrews and Westoll 1970). The latter group however appears to be paraphyletic, as its defining characters (rhomboid scales, presence of cosmine and median gular plate) are symplesiomorphies shared with other sarcopterygian groups. Most 'porolepids' have been assigned to the genus *Porolepis* (Gross 1936, 1941; Jarvik 1942, 1972; Kulczycki 1960). It is doubtful whether *Porolepis* is a monophyletic group, but as the genus is morphologically uniform, and better known than the other non-holoptychiid porolepiform, *Heimenia* (Ørvig, 1969), it can for practical purposes be regarded as the sister-group of the Holoptychiidae.

Genus DUFFICHTHYS gen. nov.

Derivation of name. After Patrick Duff, the first author to figure and discuss specimens of the genus, and Greek *ichthys*, fish.

Type species. *Duffichthys mirabilis* gen. et sp. nov., from the Upper Frasnian of Scat Craig, Elgin, Scotland.

Diagnosis. A holoptychiid porolepiform possessing the following unique characters of the lower jaw. The attachment area for the parasymphysial tooth plate is extremely large, and incorporates part of the anterior coronoid. There is no precoronoid fossa and no distinct mentomandibular 'rib'. The anterior coronoid is strongly sutured to the anterior toothless area of the dentary. The symphysial articulation is carried on a narrow flange of the mentomandibular ('symphysial flange') which also forms the anteromesial edge of the parasymphysial tooth plate attachment.

Duffichthys mirabilis gen. et sp. nov.

Plate 1, figs 1–3; Text-figs 1–5

1842 *Holoptychius nobilissimus* Duff p. 66 pl. 6, figs 1–2, *non* (Agassiz, *in* Murchison 1839).

Remarks on synonymy. Owen (1841) described four porolepiform teeth from Scat Craig as different species of *Dendrodus*, but it is impossible to determine whether these belong to *Duffichthys* or *Holoptychius*. Duff (1842) figured RMS G 1891.92.433 and 1950.38.76 under the name *Holoptychius nobilissimus*, but with serious reservations. His comments on RMS G 1950.38.76 are worth quoting in full (Duff 1842, p. 66; capitals and italics as in original):

'This jaw has been referred to the Holoptychius Nobilissimus, in which supposition I am not inclined to concur, for this reason, that I have found, in the same locality of Scat Craig, *scales of a different fish* from the Holoptychius, having on their surface tubercles or papillae, agreeing in style with those on this jaw; while I have also got occipital plates and bones of the head corresponding in style with the sculpture on the surface of the scales of the Holoptychius Nobilissimus.'

Diagnosis. As for genus.

Derivation of name. Latin, *mirabilis*, extraordinary or unusual, referring to the unique morphology of the lower jaw.

Holotype. RMS G 1891.92.433 (Figured, Duff 1842, pl. 6, fig. 2). A partial lower jaw showing symphysial region, anterior coronoid and posterior coronoid (Pl. 1, figs 1–2; Text-fig. 2A–C). Royal Museum of Scotland, Edinburgh.

Referred material. At the end of the investigation, only three further jaw fragments had been discovered; paratypes, RMS G 1950.38.76 (Figured, Duff 1842, pl. 6, fig. 1), BMNH P8268 (Natural History Museum, London) and OUM D791 (University Museum, Oxford). When this manuscript was nearly completed, however, three more lower jaws – GSM 89144 (drawer 55/6), 89158 (drawer 55/6) and 89166 (drawer 55/7) – came to light at the British Geological Survey. These have not been studied in the same detail as the principal specimens but seem to agree with them in all important respects. In addition to the jaw specimens, two possible parasymphysial tooth plates of *Duffichthys* have been found. One, BMNH P8270, is discussed in detail below; the other, GSM 89134 (drawer 55/6), appears essentially identical to the better-known specimen.

Description. The four principal specimens (Text-figs 1–3, 4G) all show the anterior part of the lower jaw, although the symphysis is only preserved in RMS G 1891.92.433. This specimen also shows the most posterior coronoid, and a natural mould of the 'primordial canal' of the Meckelian cartilage (compare Gross 1941, figs 2, 5). The present appearance of RMS G 1891.92.433 suggests that the jaw ramus was strongly curved in the vertical plane. However, the natural mould of the 'primordial canal' has been broken and repaired (Text-fig. 2A-B); a comparison with Duff's excellent figure (Duff 1842, pl. 6, fig. 2) shows that the posterior part of the jaw has been displaced dorsally and reduced in size between 1842 and the present day, presumably at the time of this breakage. The jaw ramus was originally more or less straight, as shown in the reconstruction (Text-fig. 5E). As the posterior region is poorly preserved and rather uninformative, the description will focus on the anterior part of the jaw.

The most striking feature of the jaw is the great size of the attachment area for the parasymphysial tooth plate. This is preserved in its entirety only in the holotype, where it is seen to be of a complex shape, anteroposteriorly concave but dorsoventrally convex – 'saddle-shaped' seems the most appropriate term (Text-fig. 2A). It is bounded posteriorly by a curving, crenulated edge and anteriorly by a relatively narrow flange which carries the symphysial articulation. The dorsal edge of the attachment area rises somewhat above the general level of the jaw margin. In RMS G 1950.38.76 (Pl. 1, fig. 3; Text-fig. 1B) the posterior half of the attachment area is preserved, together with the lower end of the anterior flange. In BMNH P8268 only the posteroventral corner of the attachment survives, whereas OUM D791 preserves a natural mould of the anterior part of the attachment.

The main part of the attachment is formed by the anterior toothless area of the dentary. This also contributes to the symphysial flange; in RMS G 1891.92.433 the suture between the dentary and mentomandibular components of the flange cannot be detected. The ventral suture between the dentary and mentomandibular passes through a conspicuous foramen ('foramen 1'), unknown in other porolepiforms. This is the posterior opening of a canal, most probably for a blood vessel, which emerges on the broken anterior end of RMS G 1950.38.76 ('foramen 2', Text-fig. 1B).

In RMS G 1950.38.76, where the sutures are clearly visible, it can be seen that the posteroventral corner of the tooth plate attachment area incorporates part of the anterior coronoid, which is joined to the dentary by a strongly interdigitating suture. The same is true in BMNH P8268, where the anterior coronoid carries part of the crenulated ridge, and the broken anterior edge shows some of the interdigitations of the coronoid/dentary suture.

Unlike in other porolepiforms (see below), the mentomandibular is not differentiated into a ventral 'rib' and

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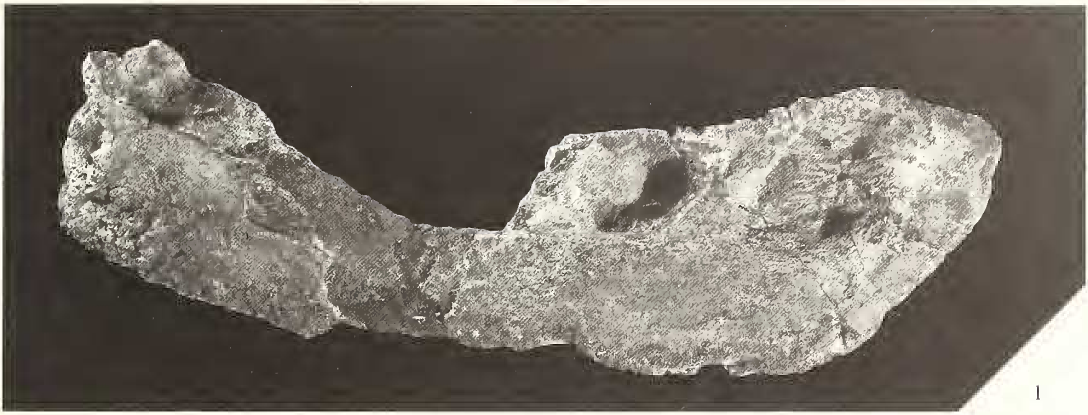
EXPLANATION OF PLATE 1

Duffichthys mirabilis gen. et sp. nov. Upper Frasnian, Scat Craig, Scotland. 1–2, RMS G 1891.92.433, holotype; partial left lower jaw, mesial and lateral views, × 1·8. 3, RMS G 1950.38.76, paratype; anterior part of left lower jaw in mesial view, × 1·8.



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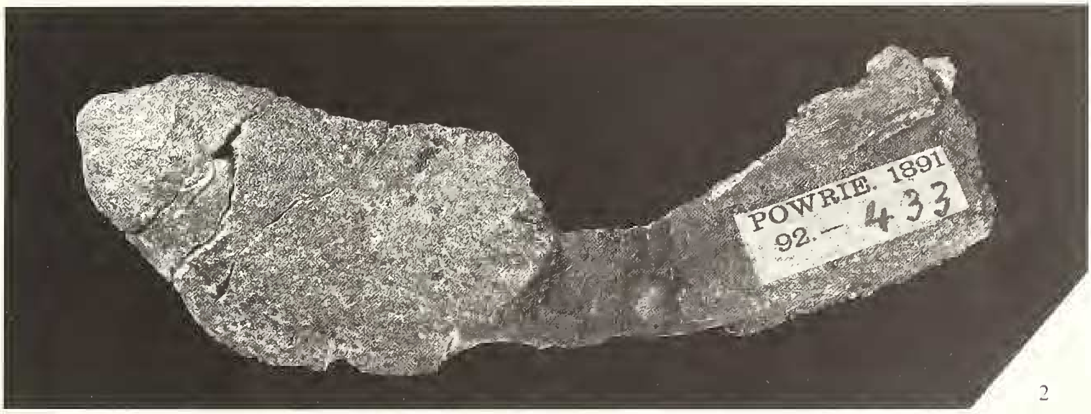

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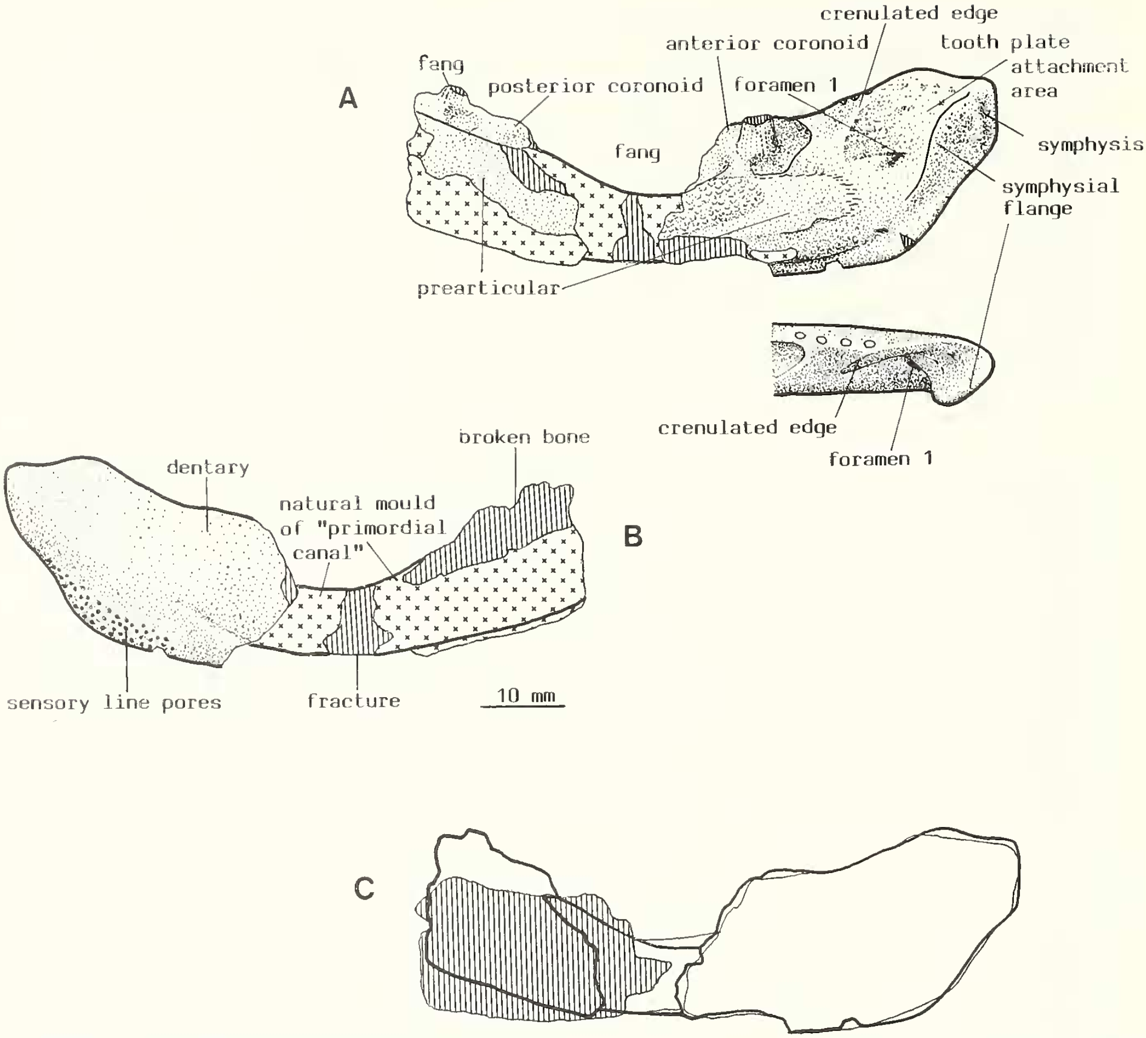
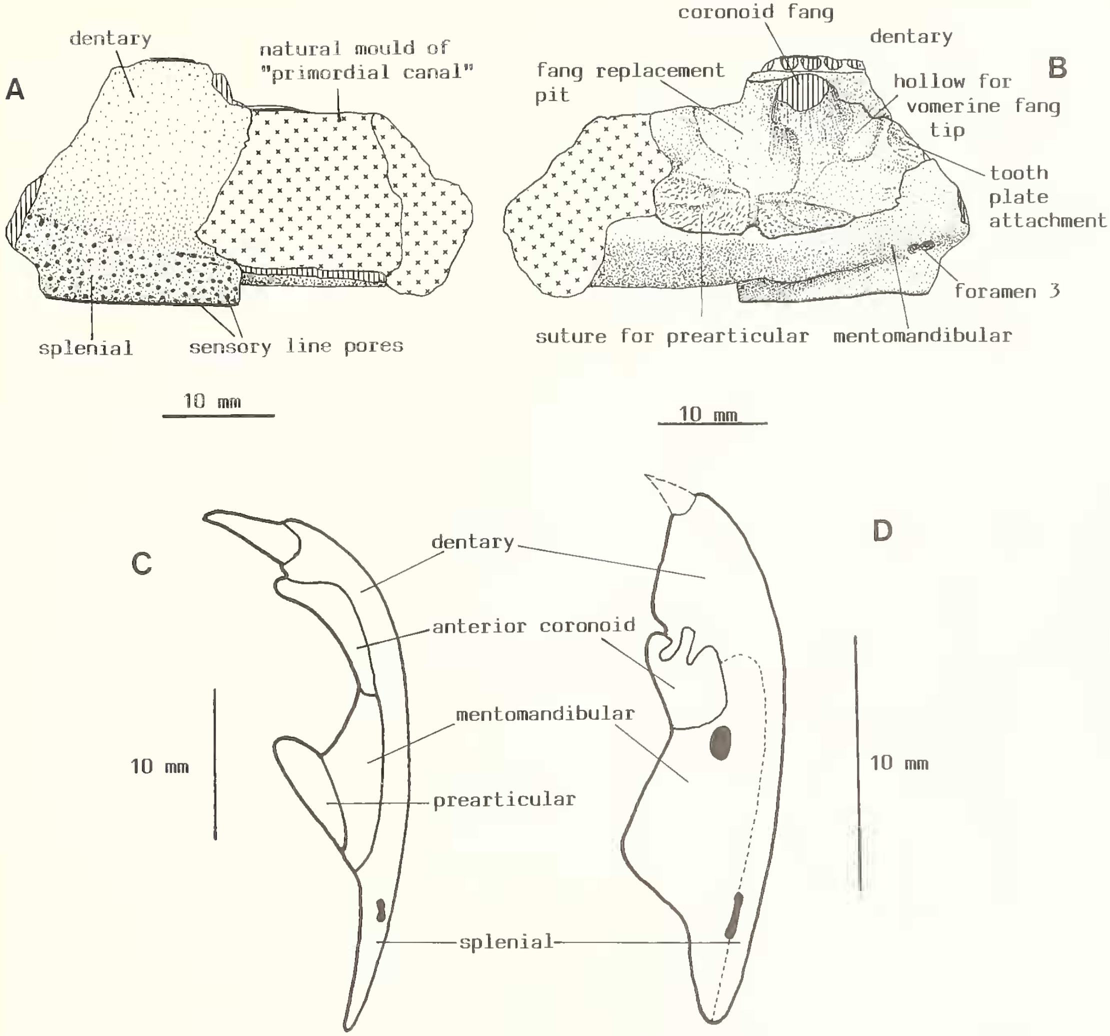
AHLBERG, *Duffichthys*



TEXT-FIG. 2. A–B, RMS G 1891.92.433, holotype of *Duffichthys mirabilis* gen. et sp. nov. A partial left lower jaw in mesial (anterior end also shown in dorsal view), and lateral views. Symbols as for Text-figure 1. C, superimposed outlines of RMS G 1891.92.233. Thick outline, present appearance; thin outline, after Duff (1842); vertical hatching, size of posterior bone block in 1842.

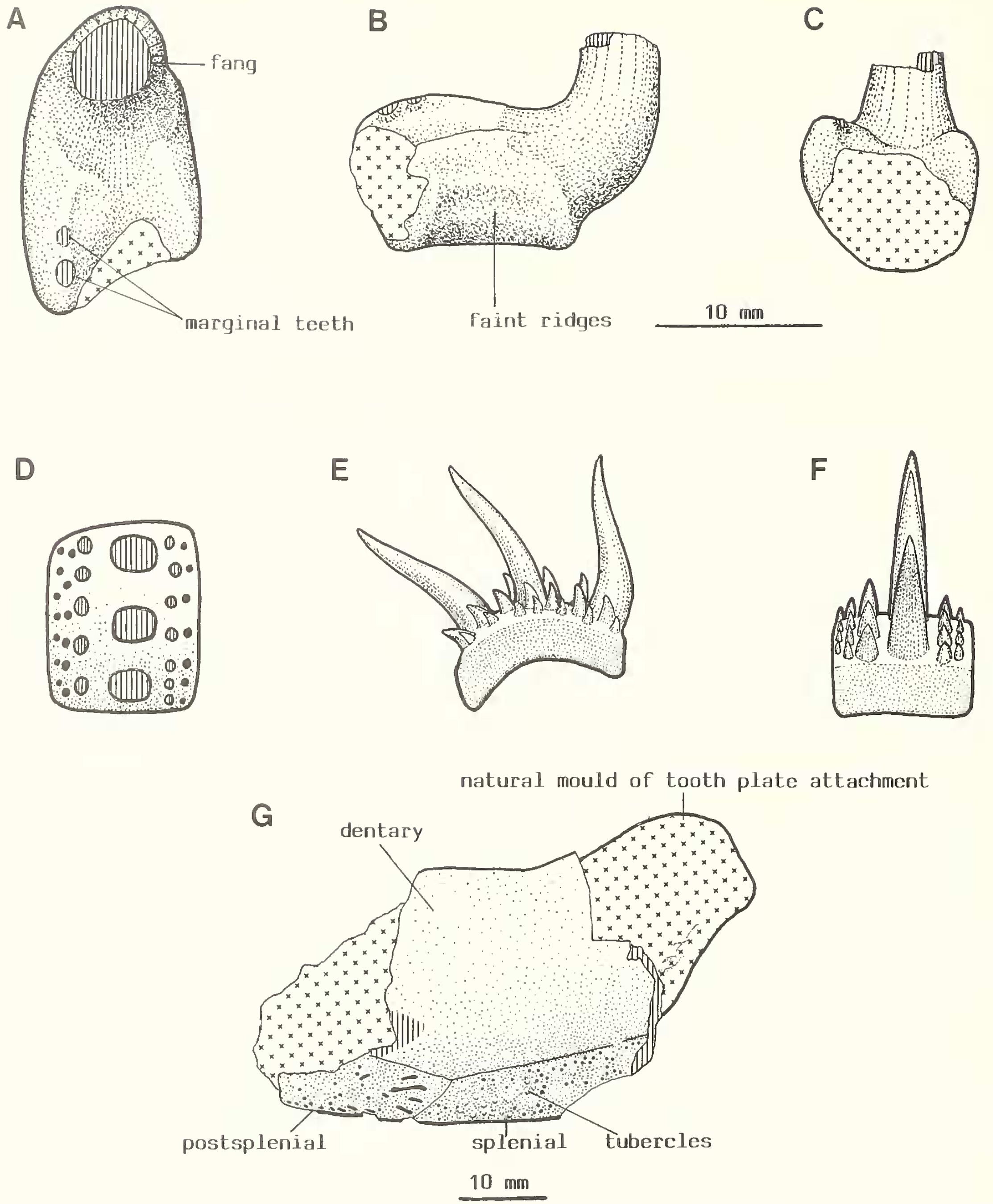
dorsal 'lamina', and there is no precoronoid fossa (Text-figs 1–3, compare Text-figs 5A–C). The coronoid/mentomandibular suture (seen in RMS G 1950.38.76 and BMNH P8268) runs anteroposteriorly, with a characteristic s-curve in the region where the precoronoid fossa would be located in other porolepiforms. RMS G 1950.38.76 and BMNH P8268 both show a small hollow on the coronoid just anterior to the fang. This hollow presumably received the tip of the vomerine fang, and is thus the functional equivalent (though not the structural homologue) of the precoronoid fossa. The main part of the mentomandibular is stout. Ventrally, it carries a conspicuous foramen ('foramen 3') which is also present in other holoptychiids (e.g. Gross 1941, fig. 2, 'ca'). Immediately anterior to this foramen arises the narrow flange which supports the symphysial articulation. The anterior part of the mentomandibular's dorsal surface is concave and forms the ventral margin of the tooth plate attachment area. The more posterior parts of the lower jaw are similar to those of other porolepiforms; intercoronoid fossae of the normal porolepiform type are preserved in RMS G 1891.92.433 and BMNH P8268. The articular region is unknown.



TEXT-FIG. 3. A–B, BMNH P8268, *Duffichthys mirabilis* gen. et sp. nov., left lower-jaw fragment in lateral and mesial views. Symbols as for Text-figure 1. C, lower-jaw cross-section of *Glyptolepis baltica*, at level of precoronoid fossa (after Gross 1941). D, similar section of *Duffichthys mirabilis*, reconstructed from broken anterior end of BMNH P8268.

The lateral face of the jaw is well preserved in RMS G 1950.38.76, BMNH P8268, OUM D791 and GSM 89158, but rather eroded in RMS G 1891.92.433, GSM 89144 and GSM 89166. It is either smooth (BMNH P8268) or ornamented with a few small tubercles (RMS G 1950.38.76, OUM D791, GSM 89158); it is uncertain whether the tubercles are composed of dentine or bone. The dentary/splenial suture is marked by a distinct furrow. In RMS G 1950.38.76, BMNH P8268 and OUM D791, the dentary is unusually deep for a holoptychiid; the infradentaries are correspondingly narrow, and completely covered by sensory line pores. In RMS G 1891.92.433 the position of the dentary/infradentary suture is uncertain. None of the specimens possesses cosmine, and neither the splenial/postsplenial suture of OUM D791 nor the angular/surangular suture of GSM 89158 carries an infradentary foramen (see RELATIONSHIPS). A reconstructed jaw in mesial view is shown in Text-figure 5E.

The possible parasymphysial tooth plate of *Duffichthys*, BMNH P8270, consists of a small asymmetrical bone bearing three teeth (Text-fig. 4A–E). The probable anterior margin (the assumed orientation is consistent



TEXT-FIG. 4 A–C, BMNH P8270, probable left parasymphysial tooth plate of *Dufficlithys mirabilis* gen. et sp. nov., in dorsal, mesial and posterior views. Symbols as for Text-figure 1. D–F, left parasymphysial tooth plate of a generalized holoptychiid, based on Jarvik (1972, pl. 26, fig. 5) and Gross (1957, pl. 6, fig. 2); aspects corresponding to A–C. In D, vertical hatching, sites of large teeth; black spots, small teeth. G, OUM D791, *Duffichthys mirabilis* gen. et sp. nov., right lower jaw fragment in lateral view. Symbols as for Text-figure 1.

with the interpretation as a parasymphysial tooth plate) is entirely occupied by the base of a large dendrodont fang. The shaft of the fang is angled at approximately 75° to the base, and is thus held vertically despite the base being attached to the anterior edge of the bone. A complete fang with a very similar base, figured by Duff (1842, pl. 6, fig. 10) as *Dendrodus sigmoides*, is sigmoidally curved, and it seems likely that the fang of BMNH P8270 was originally of a similar shape. Interestingly, the fang of BMNH P8270 is not circular in cross-section, but shows a flattened anterolateral face on the left side (Text-fig. 4A).

The rather broad posterior margin of the bone is concave. The dorsal surface carries two marginal anteroposterior ridges, of which the left carries the worn bases of two small teeth. Posterior and lateral views of the ventral surface show it to be 'saddle-shaped' – transversely strongly convex, anteroposteriorly gently concave. It carries low, smooth anteroposterior ridges and is surrounded by a moderately prominent lip. There is no indication that the bone was firmly sutured to another element. As a whole, the bone is 'bilateral' with an obvious longitudinal axis, but it is not symmetrical; the left margin is considerably longer than the right, and the left marginal ridge is higher than its counterpart.

The dendrodont nature of the fang shows that BMNH P8270 derives from a porolepiform. There are good reasons for identifying it as a parasymphysial tooth plate (see below), but it differs considerably from those of other porolepiforms. In the latter, the parasymphysial tooth plate is a small, approximately rectangular bone, the dorsal surface convex and the ventral surface concave in the anteroposterior plane (Text-fig. 4D–F; compare Gross 1957, pl. 6, figs 1–2, and Jarvik 1972, fig. 50C and pl. 26, figs 2–6). The ventral surface carries fine anteroposterior ridges, whereas the dorsal surface is covered by teeth, also arranged in anteroposterior rows. One row is enlarged into fangs; it is always mesial to the midline of the bone, and most of the subsidiary tooth rows are lateral to the fang row. These fangs differ considerably from those on the coronoids, ectopterygoid, dermopalatine and vomer. The latter are arranged in pairs, one pair on the growth centre of each bone, but as they are shed and replaced at intervals it is common to find only one fang next to an empty replacement pit (as in BMNH P8268 and RMS G 1899.92.433; Text-figs 2A, 3B); by contrast, the fangs of the parasymphysial tooth plate only ever seem to be represented by shedding pits at the extreme anterior edge of the bone (Gross 1957, pl. 6). It thus appears that individual fangs were not shed and replaced on the tooth plate; most probably, the entire tooth plate moved forward over the attachment area, with new teeth and bone being added at the posterior margin, and worn teeth shed (and bone resorbed) at the anterior edge.

The holoptychiid tooth plate (Text-figs 4D–F, 5B) carries fewer rows of teeth than that of *Porolepis* (Jarvik 1972, pl. 26, fig. 6), and the fangs are relatively larger. It is interesting to note, however, that the shape of the plate is approximately the same despite the considerable differences in the attachment area (see Text-fig. 5, and 'Comparative and functional morphology' below).

What then are the features which identify BMNH P8270 as a parasymphysial tooth plate of *Duffichthys*? Fortunately, the tooth-bearing bones of the buccal cavity are well known in porolepiforms (Gross 1941, fig. 7; Jarvik 1942, 1972, fig. 31).

The small size of the bone relative to the fang it carries immediately shows that BMNH P8270 cannot be a coronoid, dermopalatine or ectopterygoid. The normal holoptychiid vomer is of a comparable size to BMNH P8270, but this element is always firmly sutured to the ethmoid and carries a pair of fangs or a fang and replacement pit (see above). If identification as a vomer, coronoid, ectopterygoid or dermopalatine can all be ruled out, the only remaining possibility is that BMNH P8270 is a parasymphysial tooth plate. This interpretation is supported by the size of the bone, the absence of a fang replacement pit, and in particular by the smooth, slightly striated underside which does not appear to have been firmly sutured to another bone. However, BMNH P8270 differs considerably from the tooth plates of other holoptychiids in shape, and in carrying only one fang rather than a whole row. Only two porolepiforms are known from Scat Craig, *Holoptychius* (represented by numerous scales as well as lower-jaw fragments such as BMNH P4718) and *Duffichthys*. The parasymphysial tooth plate of *Holoptychius* is well known (Jarvik 1972) and is of the normal type described above (Text-fig. 4D–F), so it is far more likely that BMNH P8270 belongs to *Duffichthys*.

In fact, the ventral surface of BMNH P8270 is in most respects a 'negative' of the toothplate attachment area of *Duffichthys*, as can be demonstrated by comparing it with RMS G 1891.92.433 (Text-fig. 2A). Although BMNH P8270 represents a larger individual than RMS G 1891.92.433, and the fit is in other respects imperfect, there is a good correspondence of parts. The left margin of the bone would lie against the main part of the toothless area of the dentary, whereas the lower and shorter right margin would come to rest against the posterolateral side of the symphysial flange. The slight anteroposterior concavity of the tooth plate is matched by the slight convexity of the dentary, and the base of the fang fits into a shallow indentation in the dorsal margin of the jaw. In this orientation the flattened anterolateral face of the fang becomes parallel to the jaw margin. The imperfections of the fit can probably be attributed to individual variation, as even in the small available sample the parasymphysial regions of RMS G 1891.92.433 and 1950.38.76 differ noticeably in shape.

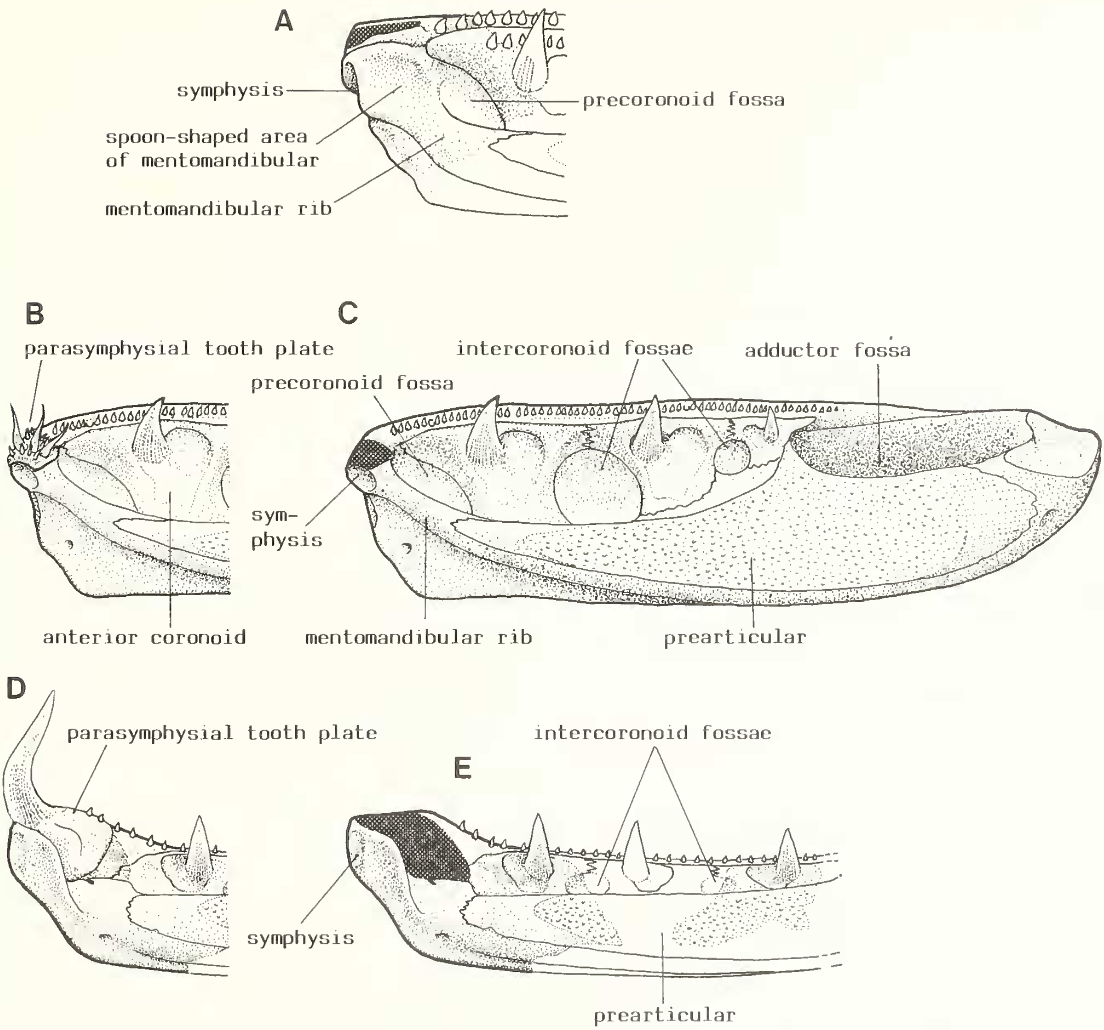
With regard to the dentition, the two small teeth on the lateral edge of the bone can be readily compared with the small teeth on the tooth plates of other porolepiforms. They appear to form an anteroposterior row, and it is interesting to note that they are lateral to the fang: in other porolepiforms (see above) there is always a greater number of subsidiary tooth rows on the lateral side of the fangs than on the mesial side, and it seems that BMNH P8270 shows a very reduced form of this pattern. The relationship of the single large fang to the row of small fangs seen in other porolepiforms is rather more puzzling. We have already seen that, in other porolepiforms, replacement of the parasymphysial teeth seems to have occurred by 'regeneration' of the entire plate (teeth being formed at the posterior margin, shed at the anterior edge) rather than the shedding and replacement of specific teeth. As BMNH P8270 only carries a single fang fused to the anterior margin of the bone, rather than an anteroposterior row of fangs, tooth replacement in this form cannot have involved continuous tooth plate growth of the kind outlined above. It is possible that the fang was shed and replaced periodically, with the tooth plate remaining in place, or alternatively that the whole tooth plate was resorbed and replaced by a new plate developing behind it. The latter interpretation accords better with the growth pattern seen in other porolepiforms, as it simply implies that the continuously growing plate has been broken up into a series of ossicles each carrying a single fang. Additional (if circumstantial) support for this interpretation comes from the concave posterior margin of BMNH P8270, which appears shaped to hold the anterior end of the next developing tooth plate.

To summarize, it can be shown that BMNH P8270 must represent a porolepiform parasymphysial tooth plate. In shape it corresponds closely to the tooth plate attachment area of *Duffichthys*, but it bears no resemblance to that of *Holoptychius*, the only other porolepiform known from Scat Craig. It thus seems reasonable to attribute it to *Duffichthys*: the only alternative is to assume that it represents a third, unknown holoptychiid with a *Duffichthys*-like jaw morphology. Text-fig. 5D shows a reconstruction of the tooth plate *in situ*. It is naturally very tentative, as the exact size relationship between tooth plate and jaw is unknown. In the reconstruction, the tooth plate does not occupy the entire length of the attachment area, and it is possible that it is shown too small. Nevertheless, it is clear that the parasymphysial fang must be very large. The construction of the attachment area gives independent evidence for the presence of a large parasymphysial fang (see below).

COMPARATIVE AND FUNCTIONAL MORPHOLOGY

Two principal lower-jaw morphologies are known in porolepiforms other than *Duffichthys*; one occurs in the primitive genus *Porolepis* (Text-fig. 5A; compare Gross 1941, fig. 23; Jarvik 1972, pl. 12, fig. 2), the other in the Holoptychiidae (Text-fig. 5C; compare Gross 1941, figs 2, 7). The posterior part of the jaw is basically similar in all known porolepiforms, although the articular region is somewhat deeper in the holoptychiids than in *Porolepis*. Similarly, the coronoids are separated ventrally by deep intercoronoid fossae (not shown by Jarvik 1972) in all porolepiforms, including *Duffichthys*. The differences between *Duffichthys*, generalized holoptychiids and *Porolepis* are concentrated in the anterior part of the jaw.

In all porolepiforms other than *Duffichthys*, a well-developed precoronoid fossa separates the mentomandibular 'rib' from the dorsal part of the anterior coronoid, and the parasymphysial tooth plate attachment is small; a comparison of cross-sections shows that the construction is much less massive than in *Duffichthys* (Text-fig. 3C, D). The form of the tooth plate attachment is the main structural difference between the lower jaws of *Porolepis* and generalized holoptychiids. In *Porolepis* (Text-fig. 5A), the toothless area of the dentary consists of a deep furrow which lies in line with the dentary tooth row. The top of the mentomandibular flares out into a spoon-shaped structure, the dorsal edge of which is overlain by a 'lip' of the dentary that supports the parasymphysial tooth plate. In holoptychiids (Text-fig. 5C), the toothless area of the dentary is broad and convex, and overlies the top of the mentomandibular; the latter is only slightly flared, not spoon-shaped. As we have seen, the tooth plates of *Porolepis* and generalized holoptychiids are quite similar, which is surprising considering the differences between the attachment areas. In holoptychiids the toothplate lies flat on the broad toothless area of the dentary, but in *Porolepis* the attachment is very narrow and it appears that only part of the plate could have been supported by the dentary, the rest presumably being held by soft tissue (it has never been found *in situ*). Neither in *Porolepis* nor in generalized holoptychiids is the anterior coronoid involved in the parasymphysial tooth plate attachment, and the attachment area is always much smaller than in *Duffichthys* (Text-fig. 5A, C, E).



TEXT-FIG. 5. A, anterior end of lower jaw of *Porolepis* sp., dorsomesial view, based on BMNH P51800. Dot shading shows extent of specimen, geometrical stipple indicates the parasymphysial tooth plate attachment. B–C, generalized holoptychiid lower jaw, with and without parasymphysial tooth plate, dorsomesial view, reconstruction based on RMS G 1859.33.17 and RMS G 1896.67.6. Geometrical stipple indicates the parasymphysial tooth plate attachment. D–E, reconstructed lower jaw of *Duffichthys mirabilis* gen. et sp. nov., mesial view, based on RMS G 1891.92.433; tooth plate based on BMNH P8270. Symbols as for A. Figures not to scale.

As can be seen, the lower-jaw structure of *Duffichthys* differs considerably from that of other holoptychiids. The typical holoptychiid jaw is a lightly built structure, essentially consisting of a thin lateral plate (the dentary and infradentaries) and a number of supporting elements on the mesial side (the Meckelian bone, coronoids and thickened dorsal margin of the dentary). The main longitudinal supporting element appears to be the Meckelian bone, the middle part of which is tubular. The coronoids are separated ventrally by deep intercoronoid fossae (Text-fig. 5C), which are usually interpreted as receiving the fangs of the dermopalatine, ectopterygoid and vomer (see for example Gross 1941). However, while the fossae undoubtedly received the tips of these fangs, they are much larger than would be necessary to fulfil that function alone. It seems probable that they also constitute a means of weight reduction. Dorsally, the coronoids are sutured together. In large individuals (such as BMNH P8266 and P4718, and RMS G 1859.33.1366), these sutures are strongly interdigitating, which is interesting as they are the only interdigitating sutures known in porolepiforms. They may have served to prevent shear between the coronoids, tying the bones together into a single structural unit. Seen as a whole, the complex of Meckelian bone, coronoids and dentary margin appear to form a type of girder composed of two longitudinal members (the Meckelian bone, and the dentary margin + dorsal parts of the coronoids) separated by crossbars (the fang-bearing parts of the coronoids).

The parasymphysial tooth plate attachment is relatively small in generalized holoptychiids, and consists entirely of the convex toothless area of the dentary (Text-fig. 5c). As we have seen, this structure is not sutured to the anterior coronoid, and it lacks raised edges or other structures for bracing the tooth plate against horizontal forces. With the tooth plate *in situ*, the parasymphysial fangs do not rise higher above the jaw margin than the coronoid fangs (Jarvik 1972, fig. 47B, C).

In *Duffichthys* the posterior part of the lower jaw seems to be of normal holoptychiid structure, but anteriorly the precoronoid fossa has been eliminated and the mentomandibular is unusually massive (Text-figs 3D, 5E). The shape of the tooth plate attachment area is also different from that of other holoptychiids in being saddle-shaped and having a raised, crenulated posterior margin. If BMNH P8270 is correctly interpreted as a tooth plate of *Duffichthys*, the parasymphysial fang was the largest tooth in the lower jaw. All these features presumably correlate with differences in jaw action and feeding behaviour between *Duffichthys* and other holoptychiids. The parasymphysial fangs do not rise higher above the jaw margin than the coronoid fangs (Jarvik 1972, fig. 47B-C). suggests they may have played a more important role in food capture than those of other holoptychiid genera.

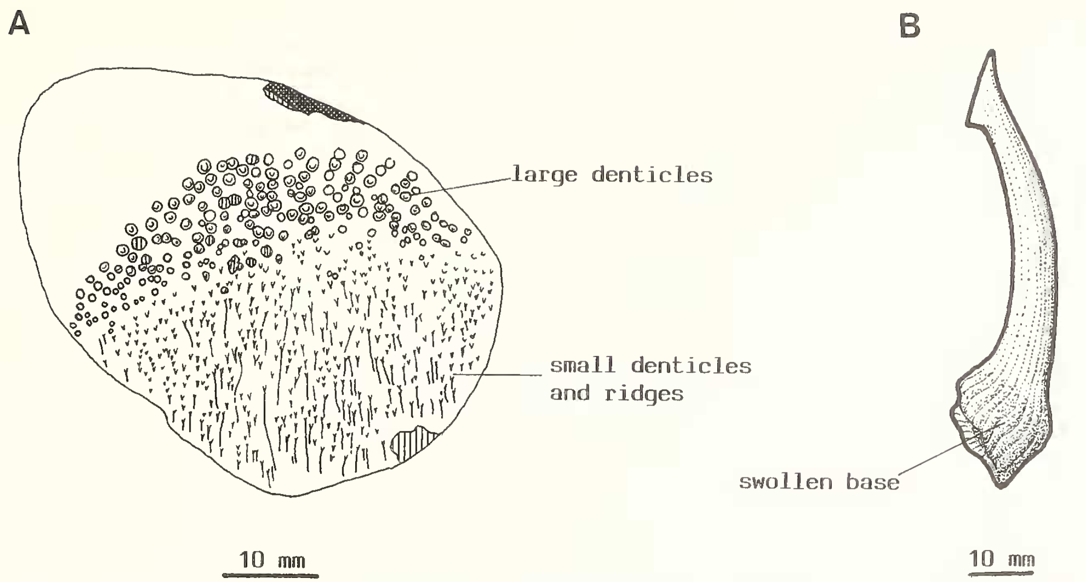
Porolepiforms are not the only sarcopterygians to show enlarged parasymphysial teeth. Onychodonts (Jessen 1966) have a large parasymphysial tooth plate with a prominent fang whorl, but lack coronoid fangs. *Eusthenodon* (Jarvik 1972, fig. 49), *Panderichthys* (Gross 1941), rhizodonts (Andrews 1985) and many early tetrapods (Beaumont 1977; Jarvik 1980) carry fangs on the anterior end of the dentary which in size, shape and mode of attachment resemble coronoid fangs. The combination of features shown by *Duffichthys*, is, however, unique among known sarcopterygians.

RELATIONSHIPS

The possession of dendrodont teeth, in combination with a lack of cosmine, identifies *Duffichthys mirabilis* as a holoptychiid porolepiform (Schultze 1969; Panchen and Smithson 1987; Ahlberg 1989). This identification is further supported by the toothless area of the dentary, which, though unique in its large size and relationship to surrounding bones, is recognizably holoptychiid-like in being broad and dorsoventrally convex. The stratigraphic position of *Duffichthys* (Upper Frasnian) lies well within the known range of the Holoptychiidae (Eifelian/Givetian boundary to end Famennian (Andrews, Gardiner, Miles and Patterson 1967)). Outgroup comparison with *Porolepis* shows that the unique characters of *Duffichthys* are autapomorphic rather than primitive for the Holoptychiidae. Unfortunately, the fragmentary nature of the material makes it difficult to determine the affinities of *Duffichthys* within the family.

Most authors (Gross 1941; Jarvik 1972, 1980) have assigned all adequately known holoptychiids and much of the fragmentary material to three genera, *Holoptychius* (Agassiz, *in* Murchison 1839), *Glyptolepis* (Miller, *ex* Agassiz 1841; formal description in Agassiz 1844) and *Laccognathus* (Gross 1941). These genera are morphologically quite similar, and were not consciously defined on the basis of derived characters. However, the generic definitions have recently been reassessed in the light of cladistic methodology (Ahlberg 1989).

Laccognathus, a monotypic genus, is chiefly characterized by its very large infradentary foramina. These foramina, the 'Kiefergruben' of Gross (1941, fig. 7B), lie on the sutures between the infradentary bones, dorsal to the mandibular sensory canal; they are not connected to the canal,



TEXT-FIG. 6. A, BMNH P8275, holoptychiid scale possibly belonging to *Duffichthys mirabilis*. Symbols as for Text-figure 1. B, tooth of *Hamodus luktevitshi*, after Bystrow (1939, fig. 8A).

and their function is unknown. The distribution of infradentary foramina among porolepiforms and related taxa is curiously disjunct (Ahlberg 1989, 1991). It is not clear whether they are primitively present in the Holoptychiidae, but the very large foramina of *Laccognathus* are unique and presumably autapomorphic. As *Duffichthys* does not possess infradentary foramina and its dermal ornament does not resemble the large, thickly enamelled dentine tubercles of *Laccognathus* (Ørvig 1957), there is no reason to believe that the two genera are closely related.

Holoptychius, which contains numerous species of very doubtful validity, mostly based on scales (Brown 1978) has a very characteristic and clearly autapomorphic scale ornament composed of laminar bone rather than dentine (Ørvig 1957). Scales of this type are among the commonest fossils at Scat Craig, and recognizable *Holoptychius* jaw fragments (BMNH P4718, P8266) also occur there. The latter are heavily ornamented and carry small infradentary foramina (compare Jarvik 1972, fig. 47C), unlike *Duffichthys*. It is possible that *Duffichthys* too carried *Holoptychius*-type scales, but the presence of a second – very rare – type of probable holoptychiid scale at Scat Craig (see below) makes this seem less likely.

Many of the characters used by previous authors (Miller 1841; Pander 1860; Gross 1930; Ørvig 1957) to characterize *Glyptolepis* appear to be primitive holoptychiid features (Ahlberg 1989), but a small clade containing the type species *G. leptopterus* can be recognized on the basis of some derived characters. One of these is extremely reduced dermal ornament on the skull bones, including the lower jaw; in some individuals the jaw carries a diffuse band of very small tubercles, but in others it is devoid of ornaments. This is essentially the same condition as in *Duffichthys*, which also resembles *Glyptolepis* in lacking infradentary foramina.

The scales of *Glyptolepis* carry dentine ornament consisting of an anterior 'fan' of small, hollow-crowned denticles in regular rows, a central area of larger irregularly arranged denticles, and a posterior field of undulating anteroposterior dentine ridges (Ørvig 1957, fig. 4B); the exposed outer bone surface of the scale is honeycomb-like, with fine, closely spaced ridges separating empty 'cells'. No scales of this type are known from Scat Craig, but Brown (1978) identified two Scat Craig scales, BMNH P8275 (Text-fig. 6A; attributed to *Holoptychius decoratus* by Traquair 1897) and P8272 'M', as specimens of 'variant' *Glyptolepis*. These scales lack the clearly defined anterior 'fan' of small denticles, and the bone surface consists of minute close-packed tubercles rather than 'honeycomb'. Brown (1978) referred these scales to *Glyptolepis* because similar scales occur on a specimen of *Glyptolepis quebecensis*, RMS G 1897.51.177, alongside the normal type described above. An isolated scale with comparable ornament, but normal 'honeycomb' bone surface, is associated with the large holoptychiid head RMS G 1964.18 (personal observation). As the lower jaw of *Duffichthys* shares some apparently derived characters with that of *Glyptolepis*, it would not be surprising to find that the former genus carried *Glyptolepis*-like scales, and it is tempting to attribute BMNH P8275 and P8272 'M' to *Duffichthys*. However, in the absence of articulated material, this identification must remain extremely tentative.

It is interesting to note that Duff (1842, p. 66) spoke of finding scales with ornament similar to that of the *Duffichthys* jaws (see systematic section above). The description suggests scales like BMNH P8275, but unfortunately Duff did not figure his specimens.

On the available evidence, *Duffichthys mirabilis* is most plausibly interpreted as forming a natural group with *Glyptolepis*, although the possibility that it carried *Holoptychius*-type scales cannot be ruled out. There are no similarities to *Laccognathus*. A more detailed assessment of relationships will probably not be possible until articulated material is discovered.

One poorly-known taxon, *Hamodus luktevitshi* (Obruchev 1933) is also relevant to the discussion of *Duffichthys*. *Hamodus* was described from the Middle Devonian of the Joglina River, Leningrad Province, on the basis of some very large (up to 90 mm long), slender, slightly sigmoid teeth with harpoon-shaped tips (Text-fig. 6B). Bystrow (1939) showed these teeth to be dendrodont, closely similar in structure to those of *Glyptolepis*. The shape is suggestive of parasymphysial fangs, but unlike 'normal' holoptychiid parasymphysial teeth, the tooth base is swollen and slightly bilobed. The angle of the base suggests that the tooth was attached to the edge of a bone in much the same way as the fang of BMNH P8270 (Text-fig. 4B), and the great size of the teeth indicates that the parasymphysial tooth plate was very large. No fangs with barbed tips are known from Scat Craig, but the points of resemblance between the *Hamodus* fangs and BMNH P8270 are suggestive, and may indicate that the former belong to an unknown, *Duffichthys*-like fish.

CONCLUSIONS

The lower jaw of *Duffichthys mirabilis*, a new holoptychiid from the Upper Frasnian of Scat Craig, Scotland, differs strikingly from those of other porolepiforms. The attachment area for the parasymphysial tooth plate is saddle-shaped and very large, and is firmly sutured to the anterior coronoid. A probable tooth plate, BMNH P8270, carries a single very large fang instead of the row of smaller fangs present in generalized holoptychiids and *Porolepis*. These features suggest that the parasymphysial dentition had a different function in *Duffichthys* than in other porolepiforms; the parasymphysial fangs may have been the principal instrument of prey capture.

Unlike the Osteolepiformes or Dipnoi, the Porolepiformes are neither taxonomically nor morphologically diverse. Only two morphological 'types' have been known until now, one represented by the primitive non-holoptychiid taxa and the other by the Holoptychiidae. Within each 'type' there is little variation. Nearly all non-holoptychiid porolepiforms can be referred to the single genus *Porolepis* (Gross 1936, 1941; Jarvik 1942, 1972; Kulczycki 1961; Jessen 1989). Among described holoptychiids there is some slight variation in the development of the marginal coronoid dentition and infradentary foramina, but skull and body proportions, and the development of the parasymphysial plate, are essentially uniform. The lower jaw of *Duffichthys*, however, diverges markedly from the generalized holoptychiid condition, presumably because the mode of feeding was different. Whether the rest of the body differed as much from those of other holoptychiids remains to be seen.

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